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THE DEVELOPMENT OF BONY PELVIC SEXUAL DIMORPHISM IN MICE

By

E. S. Crelin

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THE DEVELOPMENT OF BONY PELVIC SEXUAL DIMORPHISM IN MICE*

E. S. Crelin

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The bony pelvis of the adult human female can be distinguished from that of the adult male by a number of morphological differences.[19] Bony pelvic sexual dimorphism in the human adult was recognized early, for Vesalius,[38] in 1543, accurately described a number of morphological differences that are listed as typical of each sex in current textbooks on human anatomy. In contrast, the knowledge of a bony pelvic dimorphism in mice is comparatively recent. Gardner,[17] in 1936, performed the first experimental study on pelvic sexual dimorphism in mice. He noted a number of morphological differences between male and female pelves but focused his attention upon such differences as pubic bone resorption, increased sacroiliac flexibility, and interpubic ligament formation that occur in females during pregnancy and in virgin females and castrated males treated with estrogens. Therefore, he concluded that the dimorphism appeared following sexual maturity and indicated that estrogens played a major role in its production. Crelin and Haines[10] found that although male and female mice were gonadectomized at three weeks of age and sacrificed when adults, their pelves could readily be distinguished from each other by a number of differences, many of which were originally described by Gardner except those stated above upon which he placed the greatest emphasis.

The present investigation was designed to study the development of bony pelvic sexual dimorphism in mice in greater detail than heretofore and in such a manner that the causative factors in its production might be elucidated.

MATERIALS AND METHODS

One hundred fifty-two Brown-belt inbred mice were arranged into 5 groups:

(1) Twelve virgin females and 12 males were sacrificed at 3 months of age. Their vertebral columns from the fifth lumbar to the second caudal vertebrae and attached bony pelvis were excised en bloc and fixed in 95 per cent alcohol. At autopsy this procedure was performed on each animal in the entire experiment and the excised tissue prepared as a whole mount for detailed study as follows. The pelvic viscera, including most of the musculature, were removed. The joints with their ligaments were

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*The work described in this paper was supported in part by Grant RG-4433 from the National Institutes of Health, Public Health Service, Bethesda, Md.

maintained. Remaining soft tissue attached to the pelvic bones and vertebrae was macerated with 2 per cent potassium hydroxide and cleared in glycerin. The bones were stained with alizarin. Each whole mount was examined using a stereoscopic microscope, and various parts were measured. The pelves of Group 1 were studied to determine the characteristics that constitute constant morphological differences between the sexes in fully matured mice.

(2) Four females and 4 males were sacrificed at birth and at 3 to 4 day intervals up to 42 days and at 56 days of age (TABLE 1). The whole mounts from these mice were studied to determine the time of appearance and order of sequence of the pelvic morphological differences between the sexes during development.

(3) Twelve females and 12 males were gonadectomized at birth. They were sacrificed at 56 days of age. The whole mounts from these animals were compared with those from intact mice the same age of Group 2 to determine what effects the lack of gonadal hormones had on the development of pelvic dimorphism.

(4) Fourteen females and 14 males were gonadectomized at birth and a 2 mg. pellet of testosterone propionate was implanted subcutaneously in the dorsothoracic region of each mouse. At 14 days of age, a 5-mg. pellet was implanted in the same region in each animal. All were sacrificed at 56 days of age. The whole mounts from these animals were compared with those from mice the same age of Groups 2 and 3 to determine whether the pelvic morphology of the mice given testosterone resembled that of normal male mice.

(5) The spinal cord at the tenth thoracic vertebral level was transected in 10 female and 10 male mice at 14 days of age. At 56 days of age, the mice were sacrificed. The whole mounts of these animals were compared with those from mice the same age of Groups 2, 3, and 4 to determine whether or not the gonadal hormones influence the shaping of the bony pelvis during its development by acting on the attached striated musculature to produce differences between the sexes in muscle tension and/or the direction of its pull.

RESULTS

In the experimental groups where the pelvic morphological differences were slight between mice the same age and treated identically, the pelves from each sex and, in some instances from both sexes, are often described as one.

Group 1

The morphological differences between the pelves of adult females and males were associated primarily with a larger birth canal in the female, especially its caudal outlet (FIGURES 3 and 6). The ilia at the sacro-iliac joints in nearly all of the females were inclined ventrally at a greater angle from the longitudinal plane of the vertebral column than those of the males, so that the caudal half of the bony pelves from nearly all the females was shifted to a more ventral position (FIGURES 2 and 5). The bones forming the pelvic outlet of the female's pelvis flared outward unlike those of the male's. The transverse distance between the ischial tuberosities (intertuberosity distance) was greater in the female's pelvis (TABLE 1; FIGURES 3 and 6). The tips of the ischial tuberosities projected slightly lateral in the female's pelvis and slightly medial in the male's. The subpubic angle was greater in the females' pelves, where it averaged 40 degrees (range: 39 to 42°). In the males' pelves it averaged 35 degrees, the range being 34 to 36° (FIGURES 1 and 4).

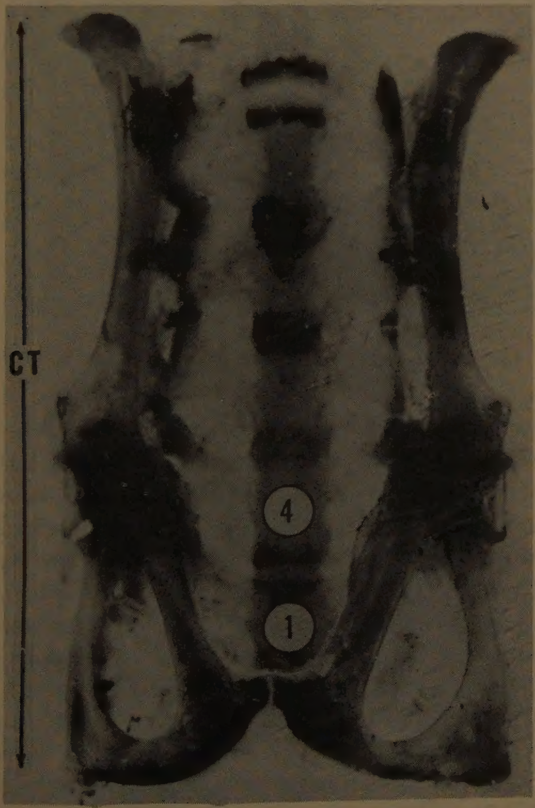

FIGURE 1. Ventral view of the bony pelvis from a 3-month-old female mouse. CT: crest tuberosity distance; 4: fourth sacral vertebra; 1: first caudal vertebra.

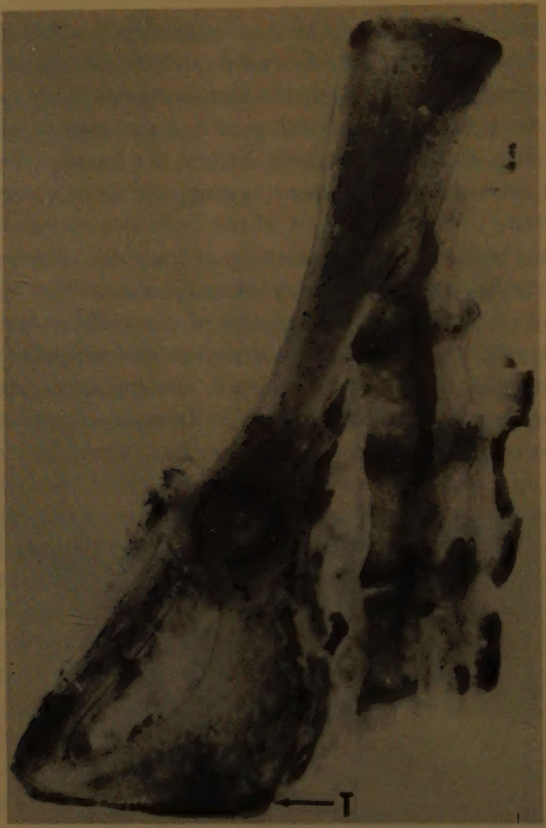

FIGURE 2. Lateral view of the pelvis shown in FIGURE 1. T: tip of ischial tuberosity.

The pubic symphysis was at a more caudal level in the female, opposite the second caudal vertebra, whereas it was opposite the first caudal vertebra in the male (FIGURES 1 and 4). This was associated with a greater length of the pubes in the females; the distance between the center of the acetabulum and the cranial border of the symphysis averaged 7.2 mm. (range: 7.0 to 7.3 mm.) in the females and 6.2 mm. (range: 6.1 to 6.4 mm.) in the males. Also, the distance between the tip of the ischial tuberosity and the caudal border of the symphysis was greater in the females, where it averaged 8.0 mm. (range: 7.9 to 8.1 mm.). It averaged 7.0 mm. (range: 6.8 to 7.1 mm.) in the males. The caudal border of the symphysis of the female's pelvis was nearly on a horizontal level with the tips of the ischial tuberosities and was partly responsible for having the pelvic outlet face directly caudally (FIGURES 1 and 2). The caudal border of the symphysis of the male's pelvis was situated more cranially than the tips of the tuberosities and was partly responsible for

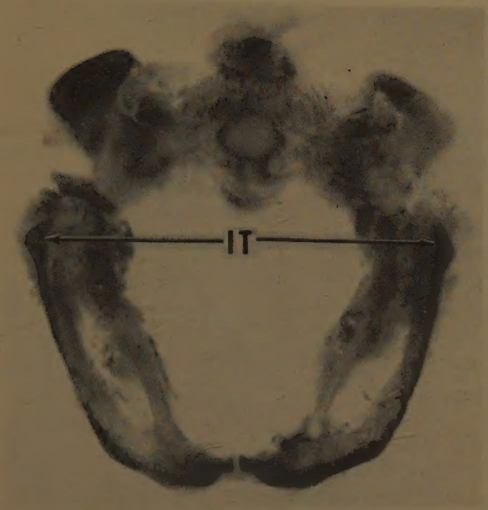

FIGURE 3. Caudal view of the pelvis shown in FIGURES 1 and 2. IT: intertuberosity distance.

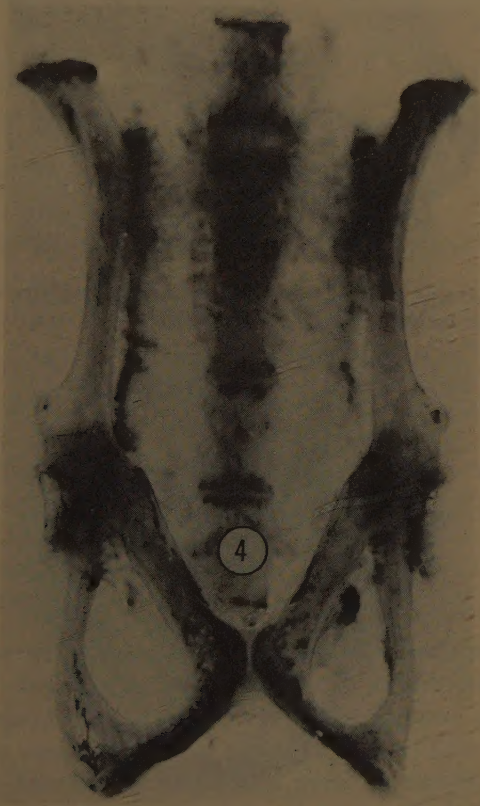

FIGURE 4. Ventral view of a bony pelvis from a 3-month-old male mouse. 4: fourth sacral vertebra.

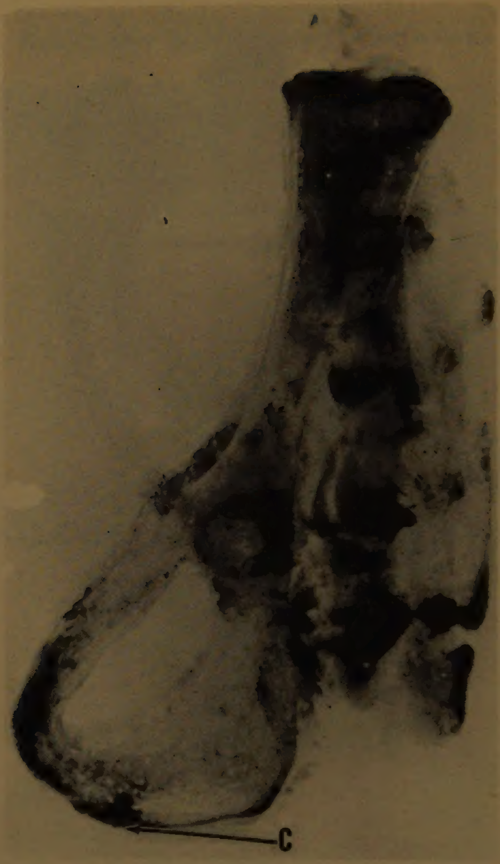

FIGURE 5. Lateral view of the pelvis shown in FIGURE 4. C: convexity of caudal border of the ischial ramus.

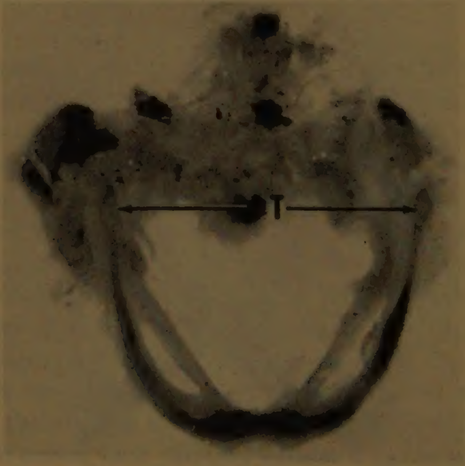

FIGURE 6. Caudal view of the pelvis shown in FIGURES 4 and 5. IT: intertuberosity distance.

TABLE 1

MEASUREMENTS OF CREST-TUBEROSITY AND INTERTUBEROSITY DISTANCES OF THE BONY PELVES FROM NORMAL MICE

No. and Sex of mice	*Age (days)*	*CT**		*IT†*	
		Average	*Range (mm.)*	*Average*	*Range (mm.)*
4 f, 4 m	1	5.0	5.0	2.0	1.8-2.2
4 f, 4 m	3	6.5	6.2- 6.8	4.0	3.8-4.2
4 f, 4 m	7	7.0	6.5- 7.5	4.0	3.7-4.3
4 f, 4 m	10	8.0	7.5- 8.5	4.0	4.0
4 f, 4 m	14	9.0	8.6- 9.3	4.0	3.8-4.2
4 f, 4 m	17	10.0	9.0-11.0	5.0	4.8-5.2
4 f	21	10.5	10.0-11.0	6.5	6.2-6.7
4 m	21	10.5	10.0-11.0	5.5	5.4-5.6
4 f	24	11.5	11.3-11.7	6.5	6.4-6.6
4 m	24	11.5	11.2-11.8	5.4	5.3-5.5
4 f	28	13.0	12.5-13.5	7.0	6.7-7.3
4 m	28	13.0	12.5-13.5	5.5	5.2-5.8
4 f	31	13.5	12.7-14.1	7.0	6.5-7.5
4 m	31	13.5	13.1-13.9	6.0	5.5-6.5
4 f	38	14.5	14.0-15.0	8.0	7.8-8.2
4 m	38	14.5	14.0-15.0	6.8	6.7-6.9
4 f	42	14.5	14.3-14.7	8.5	8.4-8.6
4 m	42	14.5	14.4-14.6	7.0	6.5-7.5
4 f	56	15.5	14.5-16.5	8.0	7.5-8.5
4 m	56	15.5	15.0-16.0	7.2	7.0-7.4
12 f	93	18.0	17.5-18.5	8.5	8.3-8.7
12 m	93	18.0	17.8-18.2	7.0	6.9-7.1

*Crest tuberosity.
†Intertuberosity.

having the pelvic outlet face in a ventrocaudal direction. A curvature of the ischial and descending pubic rami also contributed to the higher location of the symphysis in the male's pelvis and was associated with a convexity of the caudal border of the ischial rami (FIGURES 4 and 5). The ischial and descending pubic rami were not curved in the female's pelvis and lacked the convexity of the ischial rami found in the male's (FIGURE 2). In fact, approximately half of the pelves from the females had concave caudal borders of the ischial rami. In the other half they were straight.

The ascending ramus of each pubic bone in the female was slightly curved with its concavity facing ventromedially, whereas in the male each ascending ramus was straight or slightly curved with its convexity facing ventromedially (FIGURES 2 and 5). Also, the ascending rami were not as broad in the female's pelvis because their craniodorsal surfaces had undergone the typical postpuberal bone resorption. This resorption resulted in a loss of approximately the cranial half of the medial surfaces of the pubic bones at the symphysis. Thus the craniocaudal length of the symphysis averaged 1.5 mm. (range: 1.2 to 1.7 mm.) in the females and 2.8 mm. (range: 2.7 to 2.9 mm.) in the males (FIGURES 1 and 4). The narrowest point of separation between the medial ends of the pubic bones at the symphysis averaged 0.3 mm. (range: 0.2 to 0.4 mm.) in both sexes.

The size and shape of the obturator foramina were similar in both sexes. The over-all massiveness and density of the bones of both the male and female pelves were similar. The average distance between the crest of the ilium and the tip of the ischial tuberosity (crest-tuberosity distance) was the same in both sexes (TABLE 1; FIGURES 1, 2, 4, and 5).

Group 2

Newborn. The pelves of the males and females were identical. Since constant sex differences did not appear until 21 days of age, the descriptions and measurements of the pelves from the newborn and mice of subsequent ages up to 21 days refer to those from both sexes. The measurements of the crest-tuberosity and intertuberosity distances of the pelves from the newborn are listed in TABLE 1. The iliac crests, acetabula, angle, and descending rami of the pubes, and the greater part of the ischial rami were cartilaginous, whereas the main shafts of the developing pelvic bones were ossified. The cartilage from which the pubic symphysis develops was opposite the partially ossified first caudal vertebra. It consisted of a bar of small-celled hyaline cartilage that was continuous with the hyaline cartilage that is replaced by the angle and descending rami of the pubes and ischial rami at a later time in development[11] (FIGURES 7 and 8).

Three-day-old. The measurements of the crest-tuberosity and intertuberosity distances are listed in TABLE 1. The bodies of the pelvic bones destined to form the bony acetabula were partially ossified. The angles of the pubes and the ischial rami were more extensively ossified than those of the newborn. The interpubic joint of almost all the mice up to 56 days of age was located opposite the first caudal vertebra (FIGURES 9 and 10). A few pelves of both sexes had interpubic joints opposite the second caudal vertebra.

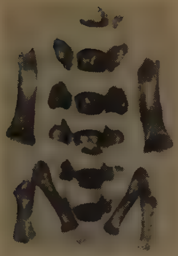

FIGURE 7. Ventral view of a bony pelvis from a newborn male mouse.

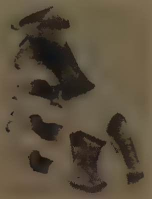

FIGURE 8. Lateral view of a bony pelvis from a newborn female mouse.

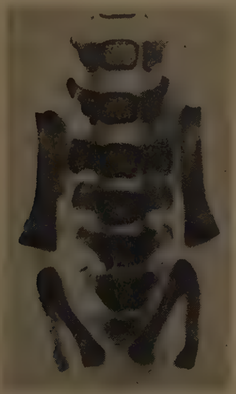

FIGURE 9. Ventral view of a bony pelvis from a 3-day-old male mouse.

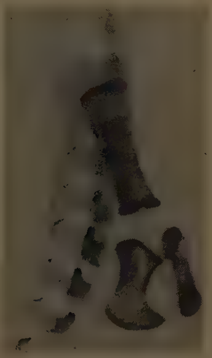

FIGURE 10. Lateral view of a bony pelvis from a 3-day-old female mouse.

Seven-day-old. The measurements of the crest-tuberosity and intertuberosity distances are listed in TABLE 1. The bodies of the pelvic bones, pubic angles, and ischial rami were more extensively ossified than in the 3-day-old.

Ten-day-old. The measurements of the crest-tuberosity and intertuberosity distances are listed in TABLE 1. The bodies of the pelvic bones were ossified so that the triradiate growth cartilage separating them at the acetabulum formed the typical T-shaped plate. The triradiate cartilage was continuous laterally as the articular cartilage of the acetabular socket. The descending rami of the pubes were partially ossified, and the ischial rami were more extensively ossified than in the 7-day-old.

Fourteen-day-old. The measurements of the crest-tuberosity and intertuberosity distances are listed in TABLE 1. The triradiate cartilage was smaller than that of the 10-day-old, due to progressive ossification of the bodies of the pelvic bones. Progressive ossification of the descending pubic ramus and ischial ramus greatly reduced the width of the growth cartilage separating the two (FIGURES 11 and 12).

Up to 14 days of age, the ilia at the sacroiliac joints in both sexes were inclined ventrally at a pronounced angle from the longitudinal plane of the vertebral column. However, in one half of the 14-day-old males this inclination was markedly reduced.

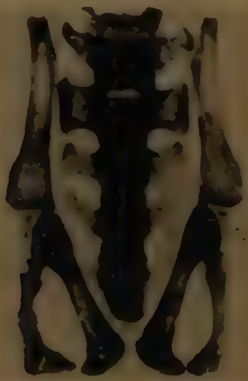

FIGURE 11. Ventral view of a bony pelvis from a 14-day-old male mouse.

Seventeen-day-old. The measurements of the crest-tuberosity and intertuberosity distances are listed in TABLE 1. The acetabular triradiate growth cartilage separating the pelvic bones was reduced to narrow plates. The descending pubic ramus and ischial ramus were fused; none of the growth cartilage that separated the two remained. In 1 male the ventral inclination of the ilia at the sacroiliac joints was much less than that of all the other 17-day-old mice.

Twenty-one-day-old. Constant morphological differences between the

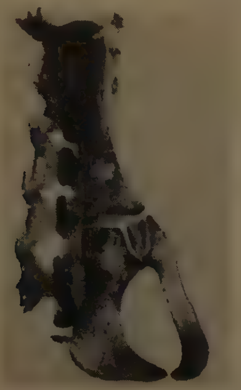

FIGURE 12. Lateral view of the pelvis shown in FIGURE 11.

pelves of the two sexes appeared for the first time during development. Although the average of the crest tuberosity distance was the same in the pelves of both sexes, the intertuberosity distance was greater in the females' (TABLE 1). The greater intertuberosity distance in the female's pelvis was associated with a flaring outward of the bones forming the pelvic outlet. Therefore, the subpubic angle was greater in the female's pelvis than in the male's and remained so from this age. Also, the tips of the ischial tuberosities pointed slightly lateral in the female's pelvis, whereas they pointed slightly medial in the male's (FIGURES 13 and 15). A distinct concavity was present on the caudal border of the ischial

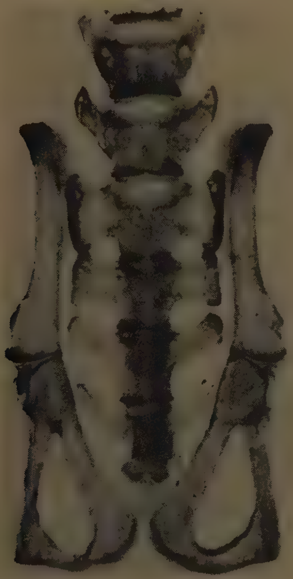

FIGURE 13. Ventral view of a bony pelvis from a 21-day-old female mouse.

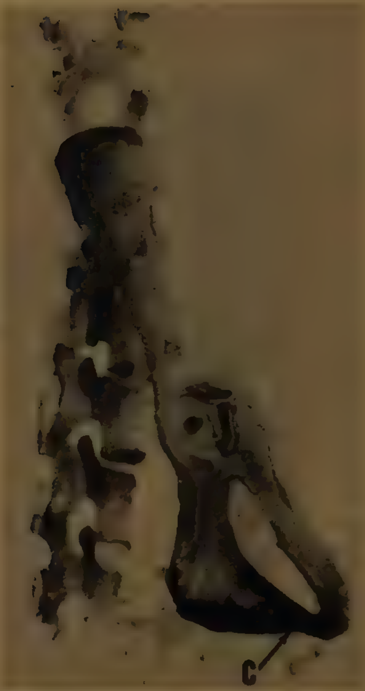

FIGURE 14. Lateral view of the pelvis shown in FIGURE 13. C: concavity of caudal border of ischial ramus.

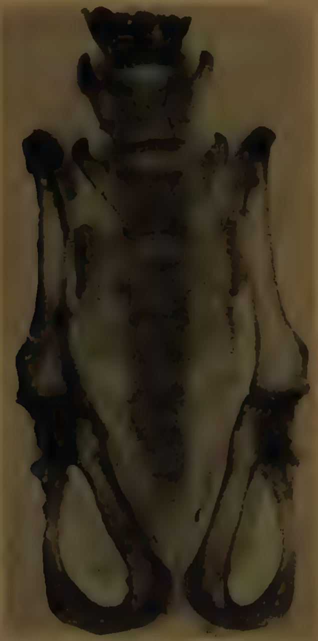

FIGURE 15. Ventral view of a bony pelvis from a 21-day-old male mouse.

rami of the female's pelvis (FIGURE 14). In the male's, the caudal border had only a slight concavity or was straight (FIGURE 16). The ventral inclination of the ilia at the sacroiliac joints in the males' pelves was less than that of all the females' except one, which shifted the symphyses of the males to a more caudal position. This reduced ventral inclination of the ilia at the sacroiliac joints of the males' pelves was a constant finding when compared with the majority of the females from 21 to 56 days of age. It was noted at autopsy and was maintained throughout the preparation of the pelves into whole mounts. A detailed study of the sacroiliac joints of the prepared specimens revealed that the manner of articulation of the bones at the sacroiliac joints were equally variable in both sexes. Few pelves were identical in the whole experiment from mice beyond 21 days of age in regard to the way the sacral vertebrae articulated with the ilia. It was not uncommon to find differences between 2 joints in 1 pelvis. Most frequently, the alae of the first sacral vertebra articulated exclusively with the ilia. In approximately one fourth of the pelves from either sex, all or a greater part of the alae of the second sacral vertebra, including those of the first, articulated with the ilia. It was not possible to ascertain differences in the surfaces of the cleared articular cartilage or the attachments of the cleared ligaments at the sacroiliac joints, which undoubtedly were responsible for the difference

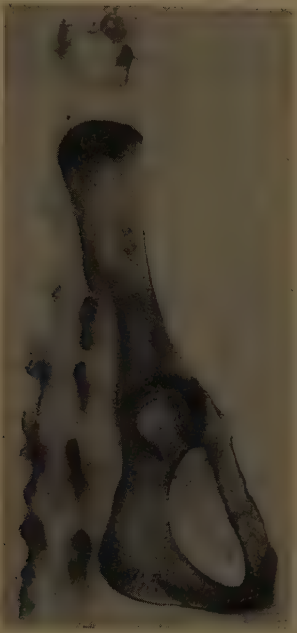

FIGURE 16. Lateral view of the pelvis shown in FIGURE 15.

between the males' and the majority of the females' pelves in the inclination of the ilia at the joints.

Twenty-four to 42-day-old. There was a progressive increase in the crest-tuberosity and intertuberosity distances of the pelves from these mice that was related to the advance in age from 24 to 42 days (TABLE 1). However, the pelvic morphology remained essentially similar to that described for their respective sex at 21 days of age (FIGURES 17 to 20). The only notable exception was that a slight convexity along the caudal border of the ischial ramus appeared for the first time during development in the 42-day-old male's pelvis.

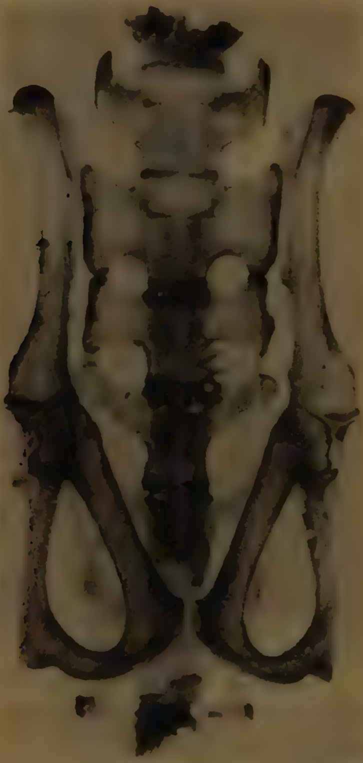

FIGURE 17. Ventral view of a bony pelvis from a 28-day-old female mouse.

Fifty-six-day-old. The measurements of the crest-tuberosity and intertuberosity distances are listed in TABLE 1. The curvature of the ascending rami of the pubes described for the 3-month-old females' pelves of Group 1 was present in the females' at 56 days of age. For the first time during development, there was a difference between the sexes in the length of the pubes. The average distance from the center of the acetabulum to the cranial border of the symphysis was 7.0 mm. (range: 6.8 to

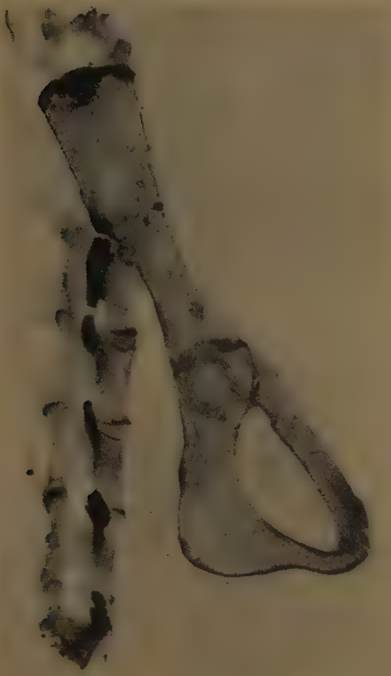

FIGURE 18. Lateral view of the pelvis shown in FIGURE 17.

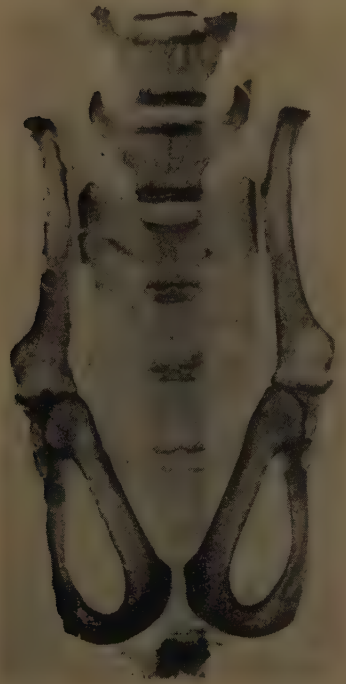

FIGURE 19. Ventral view of a bony pelvis from a 28-day-old male mouse.

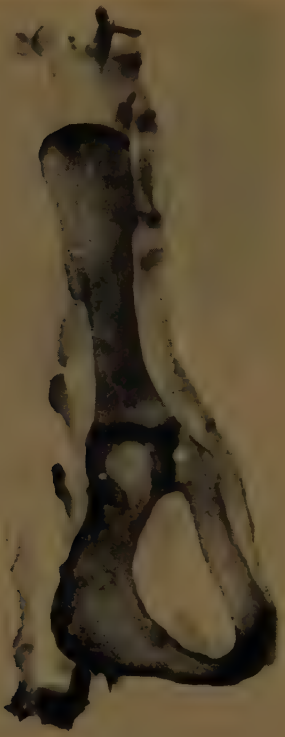

FIGURE 20. Lateral view of the pelvis shown in FIGURE 19.

7.2 mm.) in the females' pelves and 6.0 mm. (range: 5.9 to 6.1 mm.) in the males'. A definite convexity was present on the caudal border of each ischial ramus of the males' pelves and a distinct concavity in this location in each of the females'. The distance between the tip of the ischial tuberosity and the caudal border of the symphysis averaged 7.5 mm. (range: 7.0 to 8.0 mm.) in the females' pelves and 6.0 mm. (range: 6.0 mm.) in the males'. Concurrently, the symphysis shifted to the level of the fourth sacral vertebra in each male's pelvis, but it remained at the level of the first caudal vertebra in each female's.

The triradiate growth cartilage was absent in every pelvis, and some typical postpuberal pubic bone resorption occurred in each female's pelvis.

Group 3

The pelvis of each mouse gonadectomized at birth was essentially the female type both in size and morphology except that the female's pelvis lacked postpuberal pubic bone resorption (FIGURES 21 to 24). Therefore, the dimorphism of the pelvis was associated with the presence of testes.

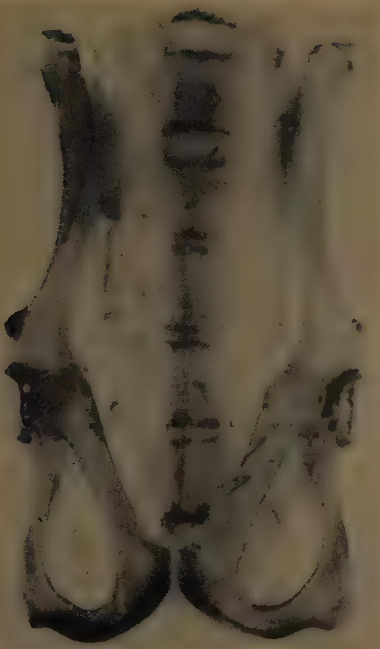

FIGURE 21. Ventral view of a bony pelvis from an 8-week-old female mouse ovariectomized at birth. It is essentially the female type.

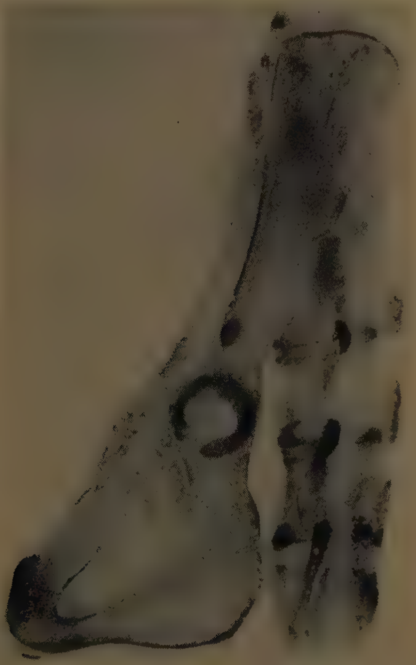

FIGURE 22. Lateral view of the pelvis shown in FIGURE 21.

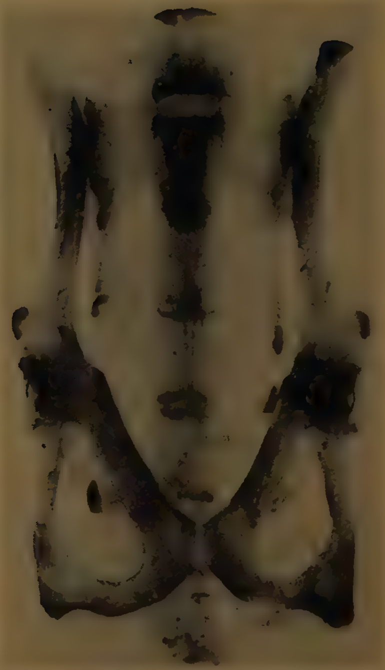

FIGURE 23. Ventral view of a bony pelvis from an 8-week-old male mouse castrated at birth. It is essentially the female type.

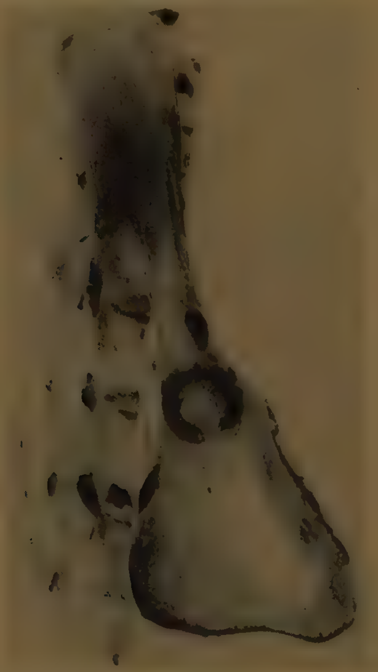

FIGURE 24. Lateral view of the pelvis shown in FIGURE 23.

Group 4

The pelves at 56 days of age of all the mice gonadectomized at birth and treated with testosterone propionate were essentially the male type with respect to both size and morphology (FIGURES 25 to 28). Thus testosterone propionate not only modified the ontogeny of the female but substituted for the intact testes of the male.

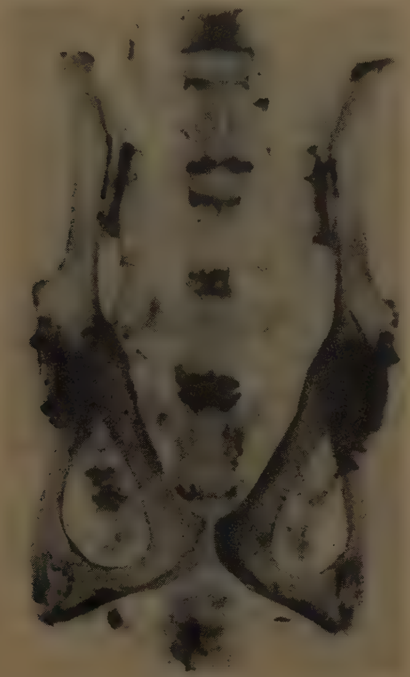

FIGURE 25. Ventral view of a bony pelvis from an 8-week-old female mouse ovariectomized at birth and treated with testosterone. It is essentially the male type.

Group 5

Three of each sex survived to 8 weeks of age after transection of the spinal cord. A major postoperative complication was urinary retention. At autopsy, the surviving mice had greatly distended urinary bladders. No pelvic striated musculature was observed at necropsy in these 8-week-old mice. Contracture tissue in 2 females and 1 male produced a scoliosis of the lumbar spine. It was difficult to dissect out the bony pelves from the mice of this group because the bones were extremely fragile.

Although the crest tuberosity and intertuberosity distances were approximately the same as those of the respective sexes of normal 38-day-old mice, each male's pelvis and each female's possessed essen-

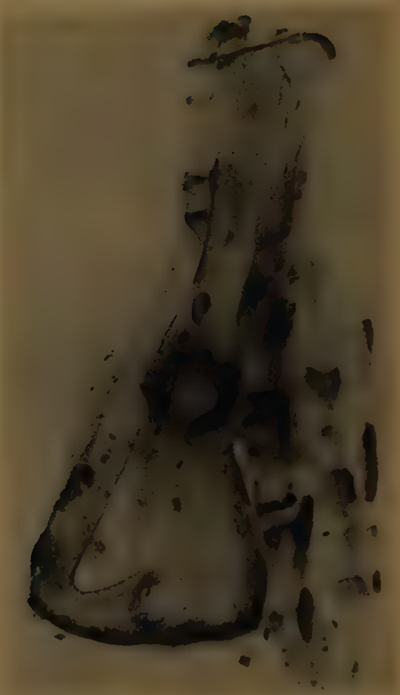

FIGURE 26. Lateral view of the pelvis shown in FIGURE 25.

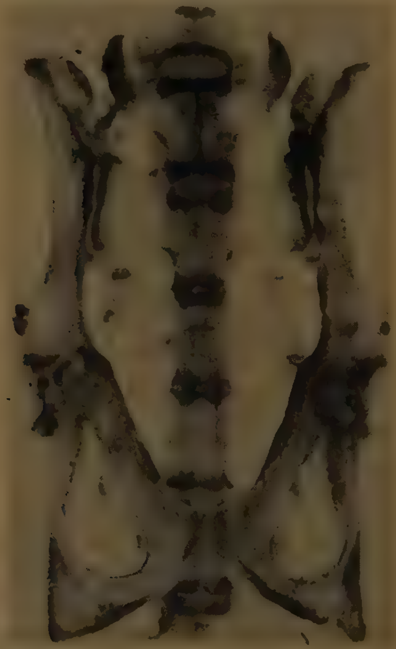

FIGURE 27. Ventral view of a bony pelvis from an 8-week-old male mous castrated at birth and treated with testosterone. It is essentially the male typ

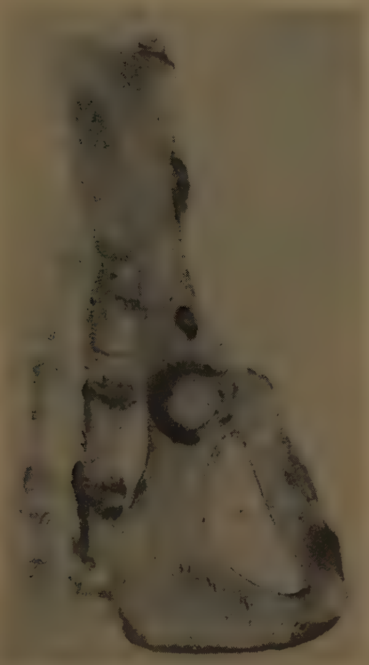

FIGURE 28. Lateral view of the pelvis shown in FIGURE 27.

tially all of the dimorphic characteristics of their respective sex found in the pelves from normal 56-day-old mice, including some postpuberal pubic bone resorption in the female's pelvis (FIGURES 29 to 32). Thus, in the absence of functional pelvic striated musculature, the male and female mice acquired dimorphic bony pelves.

DISCUSSION

The sexual dimorphism of the bony pelvis of inbred mice is more constant than that of man. One reason for this is that in man there is an individual difference in the shape of the pelvic inlet. Although the same general differences occur in the shape of the pelvic inlet of the adult human pelvis of both sexes, there are a number of constant differences which are characteristic of each sex.[36] Some of these constant differences are similar to those found in the mouse, especially the differences that contribute to a larger birth canal in the female. The developmental causative factors producing the bony pelvic sexual dimorphism in man are unknown. At birth the pelvic inlet of human male and female pelves is dolichopellic where the anteroposterior diameter is relatively longer than the transverse diameter.[36] From about 10 years of age to adulthood in human females, there is a general shift from the dolichopellic pelvic

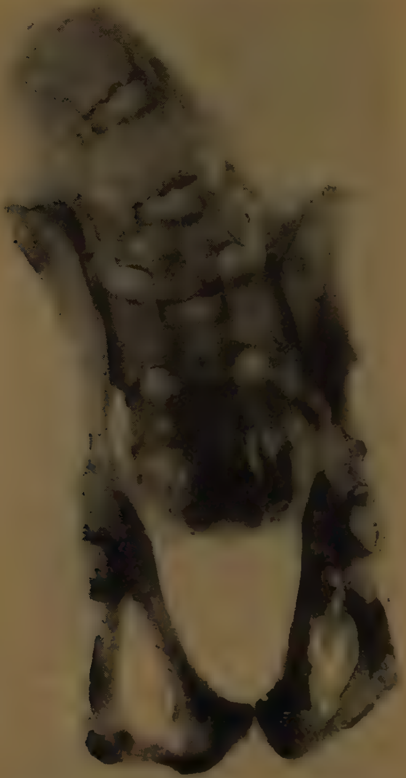

FIGURE 29. Ventral view of a bony pelvis from an 8-week-old female mouse that had its pelvic musculature paralyzed at 14 days of age. It is essentially the female type. Scoliosis of the lumbar spine is evident.

inlet to the mesatipellic where the maximum transverse diameter either equals the anteroposterior diameter or exceeds it by no more than 1 cm.[22]

The developmental causative factors producing a pelvic dimorphism in man may be similar to those of the mouse. If so, the testicular hormonal secretion would be acting to affect the shape of the pelvic bones at a comparatively earlier time in development because Thomson,[37] in 1899, found that a sexual dimorphism existed in the pelves of human fetuses as early as the fourth month of development. At this time the pelvic bones are in an early stage of ossification.[30] Thomson noted that the sexual dimorphism conformed closely to that of the adult. At the time of his report, the human anatomy textbooks generally stated that it was impossible to distinguish between the male and female pelvis until puberty. Thomson also noted that the gynecologists and investigators interested in the mechanics of the female pelvis attributed its peculiarity of growth to the effects of pressure and the influence of posture and muscula

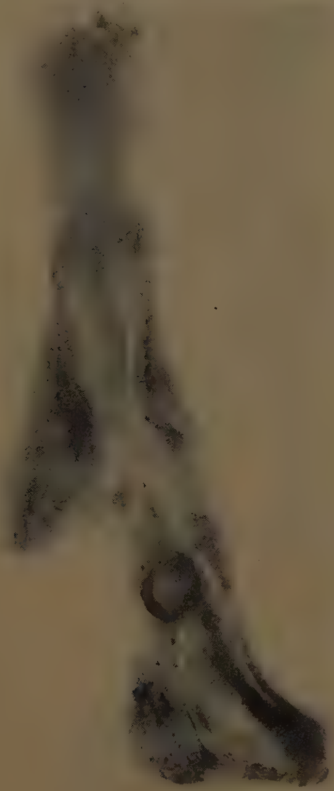

FIGURE 30. Lateral view of the pelvis shown in FIGURE 29.

action. Even though Thomson regarded the changes that take place in the position of the sacrum, the development of the sacral promontory, and the obliquity of the human pelvis to be largely dependent on mechanical causes associated with the assumption of the erect position, he felt that these influences operate alike in the two sexes and were in no way responsible for the pronounced differences found in the adult pelves. He postulated that these were due to an inherent difference in the forms of the bones and cartilage.

Greulich and Thoms[21] studied roentgenograms of 2 adult hypogonadal human males and found that each had a pelvic inlet, as well as other characteristics, which were indistinguishable in size and shape from those of many apparently normal men. These investigators stated that the masculine characteristics of the pelves in the men with hypoplastic genitalia demonstrated that male characteristics may occur even in the absence of normal testes. Although the testes in these adults were atrophic and apparently producing no androgen, they may have functioned

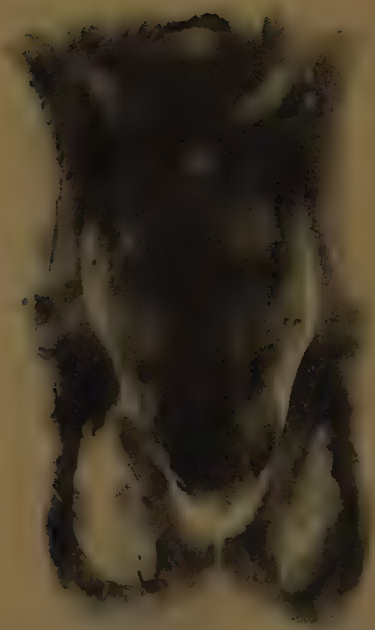

FIGURE 31. Ventral view of a bony pelvis from an 8-week-old male mouse that had its pelvic musculature paralyzed at 14 days of age. It is essentially the male type.

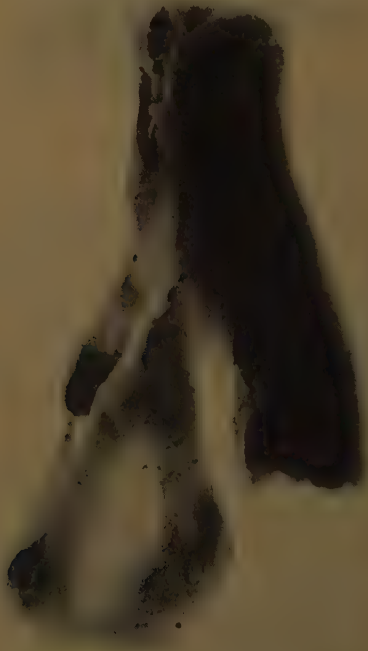

FIGURE 32. Lateral view of the pelvis shown in FIGURE 31.

during early development to modify pelvic morphology. The gonads begin to differentiate into testes in male human embryos when about 15 mm. in length, and the presumed hormone-producing interstitial cells of the testes are abundant at the fourth month of development.[1]

Failure to recognize a dimorphism when studying the pelvis of a given animal can lead to misinterpretations. Chapman[3] studied the pelves of several different burrowing animals, including the meadow and house mouse. Although the pelves of these mice are similar, he stated that they are quite different because he did not note a sexual dimorphism. The pelvis of the meadow mouse that he illustrated was obviously from a multiparous female, and that of the house mouse from an adult male. Bateman[2] studied the skeletons of normal mice and compared them with those of microphthalmic and grey-lethal mice, but did not consider a dimorphism of the pelves. He presented drawings of pubes from a microphthalmic and a grey-lethal mouse to demonstrate substantial differences in shape that he interpreted as due to differences in the time and rate of ossification. There is a possibility that sexual dimorphism was partly responsible. Harrison[24] described no dimorphism of the developing rat's pelvis. Because the rats' pelves are sexually dimorphic,[8] he might have found differences in the shape of the pelvic bones, which he did not record, if the sexes had been dealt with separately. Harrison[25] also investigated the caudal migration of the ilia in the rat during pelvic growth and again did not describe a pelvic dimorphism. Bilateral removal of the iliac crests in young rats retarded iliac growth and greatly reduced the descent of the ilia at the sacroiliac joints. One of the criteria he used was the more cranial position of the pubic symphysis, in relation to the vertebrae, of the operated animals when compared with unoperated controls. One of the morphological differences between the sexes in the rat is that the symphysis is located at a more cranial vertebral level in the male.[8] A photograph showing one of Harrison's operated rats' pelves was undoubtedly that of a male; another showing one of his control pelves was obviously that of a female.

A sexual dimorphism of the bony pelvis in rats was apparently not reported prior to 1957,[8] although a number of detailed studies have been made on the rat skeleton.[13,20,32,33,35] The pelvic dimorphism in the rat was similar to that of the mouse except: (1) The symphyses of the female rats' pelves were opposite the first caudal vertebra and, in the males', they were opposite the caudal half of the fourth sacral and the cranial half of the first caudal vertebrae; (2) the caudal border of the ischial ramus lacked a convexity in male rats; (3) the obturator foramina were smaller in the males; (4) the pelvic bones were larger in the males; (5) the pubes of both sexes lacked the curvatures found in the mouse; (6) there was no difference in the position of the ilia at the sacroiliac joints between the sexes in the rat and no postpuberal resorption of the pubes occurred in the females; (7) increased flexibility of the sacroiliac joints and interpubic ligament formation did not occur in the rat during pregnancy as they did in the mouse;[7,8,12,23] (8) the rat's pelvis, unlike that of the mouse, had a bluntly pointed projection along the dorsal border of the body of the ischium that was larger in the male's pelvis; (9) the iliopectineal eminences were more pronounced in the male than in the female rat's pelvis.

Harrison's[26] most recent publication was a brief report of a study in which he confirmed the observations that there are pelvic morphological differences between the sexes in the rat. Harrison found that the measurements of the pelves from the males were significantly greater than those of the females and that the upper margin of the symphysis lay at a lower vertebral level in the female. However, he made no mention of the other sex differences of the pelves. He gonadectomized rats of both sexes between the fortieth and fiftieth days of life and compared their pelvic dimensions with those of intact littermates. Castration had no significant effects on pelvic growth in the male but the lengths of the innominate bone, sacrum, and symphysis in the females were significantly greater in the spayed females. It could be that ovarian hormone inhibits the action of growth hormone. If so, ovariectomy allowed the pelvic bones of the ovariectomized females to attain a larger size than those of intact females. Previous studies on the rat would support this assumption.[18,34] The larger pelvis of the male rat apparently is not reflected in relative skeletal weight.[13] It is possible that gonadectomy at forty days of age was much too late to modify pelvic growth in the rat to materially alter the development of sexual dimorphism in regard to pelvic bone shape. Gonadectomy at birth in mice of both sexes did not modify the normal size of the pelvic bones, at least up to sexual maturity, because the bony pelves were approximately the same size in adult mice of both sexes.

There are two categories of pelvic sexual morphological differences in mice. One category consists of differences occurring before sexual maturity, and the other consists of those occurring after sexual maturity. The postpuberal differences, that is, pubic bone resorption, increased flexibility of the sacroiliac joints, and interpubic ligament formation are induced in the female by its ovarian hormonal secretion.[17] The postpuberal development of an interpubic ligament during the first pregnancy increases the size of the birth canal by allowing a wide separation of the pubes. However, parturition can occur without this separation of the pubic bones.[6]

In mice, the male-type pelvis occurred in females ovariectomized at birth and treated with testosterone. Conversely, the postpuberal differences that normally occur in the female were produced in the castrated male treated with estrogen or estrogen and relaxin.[4,5,17]

An immature but definite symphysis appears at three weeks of age in mice[11] that coincides with the appearance of morphological differences of the bony pelvis during development. The prepuberal dimorphism of the bony pelvis in mice developed normally even when males and females were gonadectomized at three weeks of age.[10] Therefore, the developing bony pelvis must be conditioned by the testicular hormones some time between birth and three weeks of age. The time following birth when the male can be castrated and not have its pelvis undergo the male type morphological changes is under investigation.

The cartilage of the pubic symphysis is also conditioned during development by gonadal secretions.[9] When adult male and female mice, gonadectomized at birth, received identical estrogen and relaxin treatment as adults gonadectomized when sexually mature, the response of the symphyseal cartilage to undergo ligament transformation was 50 per cent greater in males castrated when adults. Conversely, females ovariectomized when adults showed a 240 per cent greater response than females ovariectomized at birth.

The undifferentiated mesoderm of the future pelvic bones in the mouse probably has an inherited capacity to form its cartilage models. At least *in vitro* culture of a skeletal rudiment of a limb bud from a 4-day-chick embryo, consisting of a Y-shaped mass of mesoderm in which cartilage was not yet present and with no sign of the future knee joint, developed a characteristically shaped joint.[15] The constituents of the cartilage models of the future pelvic bones probably possess the capacity to predetermine the shape of the future bones. When isolated femora from 6-day-chick embryos composed of a very simple type of cartilage that showed no hypertrophied cells and no differentiation into epiphysis and diaphysis were cultivated in tissue culture, they showed self-differentiation.[16] The explanted femora underwent normal histological differentiation. Periosteal bone and a periosteal membrane formed as they grew to more than 3 times their original length. During this growth the gross anatomy of the femora remained comparatively normal.

The predetermined shape of the bony pelvis in mice would be the agonadal type that is the female type. During development of the bony pelvis, testicular hormonal secretion alters the predetermined pattern of the shape of the pelvic bones from the agonadal or female type. This secondary hormonal influence becomes irreversible at some time during the interval between birth and 21 days of age.

The basic pattern of pelvic bone shape contributing to morphological differences between the sexes was not materially altered by denervation of the pelvic musculature. It was not an unexpected finding because organ culture of explants of avian sternum formed a keel, although smaller than normal, in the absence of pectoral musculature for which it normally serves as an attachment.[14] Also, in tissue culture a knee joint developed in the cartilage model of the embryonic chick's limb rudiment that was free of muscular, nervous, and vascular influence.[15]

Studies on sexual dimorphism corroborating the present one have been made in ducks, where the agonadal type syrinx and genital tubercle is the male type. When the embryonic duck was ovariectomized, these structures developed into the male type. If, following ovariectomy, the embryos were treated with estrogen, the syrinx and genital tubercle developed into the female type.[40] When embryonic female ducks were hypophysectomized by decapitation, the syrinx and genital tubercle developed into the agonadal or male type.[28] It is probable that the release of testicular hormone during development to induce the formation of the male type pelvis in mice is also governed by the gonadotrophic activity of the hypophysis.

Wolff and Wolff[41] removed the syrinx rudiment from duck embryos at different stages of development and cultivated it *in vitro*. If the rudiment was explanted at the ninth day when the sexual differentiation of the gonads was established, it developed according to the sex of the embryo from which it was taken. When it was removed from both males and females and explanted before that stage, the syrinx differentiated into the agonadal or male type. If, however, estrogen was added to the culture medium, the syrinx acquired the female shape regardless of the sex of the donor. A massive dose of testosterone propionate added to the medium had the same feminizing effect as the female hormone. Wolff and Wolff attributed this to an inhibitory influence on the growth of the syrinx, since they could produce the same results with culture media deficient in various nutrients. It is their opinion that estrogen normally acts in an inhibitory manner on the growth and differentiation of the syrinx in female ducks because the female type is more delicate and symmetrical than the male type. It is difficult to imagine androgen having an inhibitory effect in influencing the development of the sturdy bony pelvis in male mice. Also, the 17-to-21-day postpartum onset of pelvic dimorphism in mice cannot be correlated with the differentiation of the testes, because this occurs between 11½ and 12 days of embryonic life.[31] Macintyre[29] found the testis had begun to differentiate in the 15-day-old embryo rat and produced evidence that it secreted androgen. Therefore, one might infer that the prenatal mouse testes secrete androgen in gradually increasing amounts until a threshold level is attained sometime between birth and 21 days of age to influence the subsequent shape of the developing bony pelvis.

If self-differentiation of secondary sex characters continues into the phase of sexual dimorphism, it follows the pattern of the isogametic genetic type.[39] In mammals the female type gonaducts and external genitalia is assumed in the absence of gonads, by self-differentiation, regardless of the chromosomal constitution.[27] Since the agonadal-type bony pelvis in mice was the female type, it also follows the mammalian pattern of the isogametic genetic type. Thus the agonadal type syrinx and genital tubercle in the duck is the male type because in this species it is the isogametic genetic type.[39] If a similar genetic influence determines the agonadal type bony pelvis in the rat and man, then their agonadal type would be female. In addition, the possibility is great that their bony pelvic sexual dimorphism is also the result of testicular hormonal secretion during development to produce the male type pelvis.

SUMMARY

The bony pelves of adult male and female mice have a number of constant morphological differences that, in general, cause the female pelvis to have a more spacious birth canal.

Constant pelvic morphological differences between the sexes in mice first appear between 17 and 21 days of age.

Male and female mice gonadectomized at birth have female type pelves when sexually mature. Therefore, the female type is the agonadal type and the presence of the testes is necessary for the development of the male type bony pelvis.

Male and female mice, gonadectomized at birth and treated with testosterone propionate during development, have male type pelves when adults, which indicates that androgen is the factor responsible for the production of bony pelvic sexual dimorphism.

Mice of both sexes that had their spinal cords transected at the tenth thoracic vertebral level before the appearance of pelvic dimorphism possessed the typical pelvic dimorphism when sexually mature, which demonstrates that during development the testicular hormonal secretion can produce the male type pelvis in the absence of functional pelvic musculature.

The possible genetic basis and mode of hormonal action in the production of bony pelvic sexual dimorphism is discussed along with the relationships the pelvic dimorphism of mice has to that of the rat and man.

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